

WOLF SPIDER (ARANEAE, LYCOSIDAE) MOVEMENT ALONG A POND EDGE

Lily Ahrens¹ and Johanna M. Kraus^{2,3}: Department of Biology, University of Virginia, Charlottesville, Virginia 22903, USA

ABSTRACT. Wolf spiders (Araneae, Lycosidae) are important predators at freshwater-forest ecotones where their distribution may be determined by their ability to respond to, amongst other factors, moisture and prey levels. The purpose of this study was to examine the movement of wolf spiders along a pond-forest boundary at Mountain Lake Biological Station, Virginia. We performed two mark-recapture studies at two temporal and spatial scales (4 h–20 d and 1 m–20 m, respectively) to determine the probability of movement by the spiders. Mark-recapture studies are useful for measuring individual movement, but, because of the difficulty of marking small arthropods, are not often used for spiders. This mark-recapture study showed the spiders moved very little over the temporal and spatial scale used: 0–54% per day chance of moving to the adjacent 1-m² plot around the pond and 0–2% per day chance of moving to the adjacent 1-m² plot to and from the pond. This finding is in contrast to other studies that have shown wolf spiders to completely exit a 900-m² quadrant within several days. We discuss possible causes of this low mobility and its implications for wolf spider distribution and abundance at the pond edge.

Keywords: Mark-recapture, freshwater ecotone, Pollock's robust model

Animals move to find favorable physical conditions, food and mates, for dispersal and to avoid predation (Jones 1977; Henschel 2002; Ramos et al. 2004). Both empirical and theoretical studies have long recognized that the effect of an abiotic or biotic factor on the distribution of an organism is greatly influenced by the scale over which that organism moves (Cain 1985; Hanski 1998; Weins 2001). Understanding the ability and propensity for individuals to move is, therefore, a prerequisite for predicting the response of a species to changing resources and physiological conditions (Morse 2000; DeVito et al. 2004). The usefulness of mark-recapture methods for estimating population parameters are well-known (Nichols 1992), but are not often used to quantify movement of small arthropods.

Habitat boundaries are common in nature. These boundaries or interfaces offer a large amount of variation in biotic and abiotic factors. At the freshwater-terrestrial interface,

moisture and food have been shown to vary and may influence the distribution of various consumers (spiders: Graham et al. 2003; Power et al. 2004; beetles: Hering & Platchter 1997; birds: Murakami & Nakano 2002). For example, a decline in lizard population density has been observed near a river's edge when the inputs of aquatic insect prey are experimentally reduced (Sabo & Power 2002). At a freshwater pond edge, moisture had a positive association with 3 of the 4 spider species measured (Graham et al. 2003). At the edge of a forest stream, a connection was found between flooding frequency and litter habitat, which affected the stratification of spiders along the edge (Uetz & Unzicker 1976). Information about movement gives insight into the relative importance of these factors in driving the abundance and distribution of consumers at freshwater-terrestrial interfaces.

Spiders are found in high densities in most terrestrial habitats (Moulder & Reichle 1972), and many live near aquatic-terrestrial interfaces (Nørgaard 1951; Kato et al. 2003; Kraus & Morse 2005). At this interface, moisture and desiccation tolerance are important factors influencing wolf spider distribution (DeVito & Formanowicz 2003; Graham et al. 2003). Some wolf spiders species, including repre-

¹ Current address: St. Olaf College, Northfield, Minnesota 55057, USA.

² Current address: Washington and Lee University, Lexington, Virginia 24450, USA.

³ Corresponding author. E-mail: KrausJ@wlu.edu

sentatives of the genus *Pirata*, which are found in our study area, can walk and therefore hunt on water as easily as on land (Foelix 1996).

Aquatic insects can also influence the distribution of wolf spiders near the water's edge (Henschel et al. 2001; Power et al. 2004; Kraus 2006). Wolf spiders prey on flies and other small invertebrates in the riparian zone including aquatic insects that emerge onto land (Henschel et al. 2001). The life stage, sex and physiological constraints of the spider, however, strongly affect its ability to respond to changes in prey availability (DeVito et al. 2004; Power et al. 2004). Male wolf spiders are often more active than females when searching for a mate (Framenau 2005), while juvenile fishing spiders move more frequently than adults to search for food (Kreiter & Wise 1996). Finally, spider species that desiccate more easily are constrained to certain microhabitats, and thus their movements should be limited to these habitats (Devito et al. 2004).

The purpose of this study was to determine the scale and pattern of wolf spider movement in response to differences in the biotic and abiotic environment that occur around a small pond. This was accomplished by monitoring the movement of wolf spiders (Araneae, Lycosidae) in the area surrounding a small pond in the southern Appalachians. We used mark-recapture to track cohorts > 0 –3 m from and > 0 –20 m around the pond perimeter. We hypothesized that the spiders would move laterally around the pond, but not much away from or towards the pond due to their close association with water.

METHODS

Study site and sampling design.—The study was conducted around a pond at the Mountain Lake Biological Station in the Allegheny Mountains of southwestern Virginia (37.38°N, 80.52°W, elev. 1,160 m). The shallow pond in our study site, Sylvania (70 m perimeter) was fishless. The edge of the pond was fairly well defined. There was a grassy area directly surrounding the pond and beyond that was forest, with mainly oaks (*Quercus alba*, *Q. rubra*) and pines (*Pinus rigida*). The common wolf spider species found at this study site include *Pirata cantralli* Wallace & Exline 1978, *Pirata montanus* Emerton 1885, *Pirata sedentarius* Montgomery 1904, *Par-*

dosa milvina Hentz 1844 and *Pardosa moesta* Banks 1892. Voucher specimens have been deposited at the Smithsonian National Museum of Natural History, Washington, DC, USA. *Pirata cantralli* and *P. sedentarius* both appear to be water specialists (DeVito & Formanowicz 2003; this study), while *P. milvina* inhabits open habitats (Marshall et al. 2000) and *P. moesta* has more general affinities including forested and wet areas (Buddle 2000). *Pirata montanus* lives in leaf litter (Pearce et al. 2004), and in this study was constrained to one area of the pond where the slope aspect was steep and trees and shrubs grew closer than 3 m from the water's edge.

We performed an initial mark-recapture analysis to find the approximate detection probability. In each of two 1 m² plots, LA visually searched for wolf spiders for 20 minutes, marked, released and waited one hour before searching again. We found a 15% detection probability in one plot and 26% in the other. While this was lower than some recapture rates for wolf spiders (Framenau & Elgar 2005, $> 30\%$ recapture rate), it is comparable to the recapture rate found by Kiss & Samu (2000) (5–19% recapture rate), and is high enough to estimate movement probability with sufficient accuracy. To test that the plot remained a closed system during the 1 h before recapture, one of us (LA) visually monitored three wolf spiders (one female with egg sac, one adult male, and one juvenile) for 0.5 h and found that each moved 8 cm or less.

We estimated movement rates of wolf spider cohorts using two randomly placed grids that were comprised of nine rectangular or square plots each located around Sylvania Pond (Fig. 1). "Dispersed Grid" (D1-D3, Figure 1), begun 14 June 2004 at the northeast side of the pond, had nine plots split into three separate columns. Each column consisted of three 1 × 3-m plots located adjacent and parallel to the pond edge. Movements between plots in a column therefore required that the spiders moved at least > 0 –3 m. Columns were 8–11 m apart, requiring spiders to move at least 8–28 m to reach another column. They were equidistant from existing structures from another study (Kraus 2006). "Adjacent Grid" (A on Fig. 1), begun 28 July 2004 on the northwest side of Sylvania Pond, consisted of nine adjacent 1 × 1-m plots, set in a square formation. In this case, for spider movement

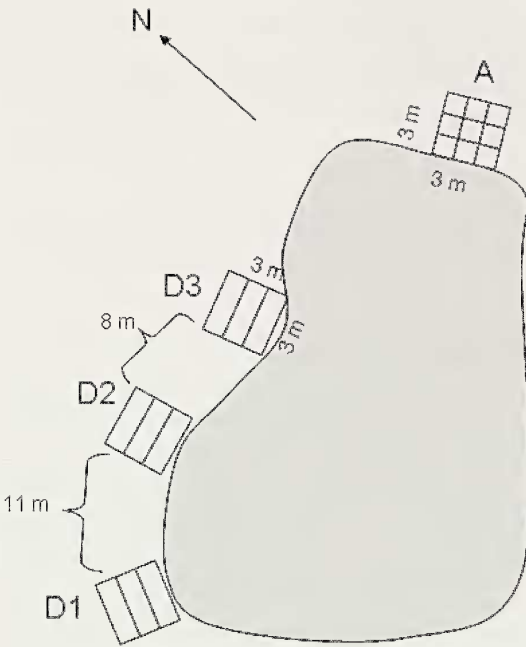


Figure 1.—Diagram of Sylvatica Pond. The two grids, each containing 9 plots, represent the plots used for the mark and recapture of this study (A, D1-D3). The plots of “A” (Adjacent Grid) are 1 × 1 m and the plots for “D” (Dispersed Grid) are 1 × 3 m.

perpendicular or parallel to the pond edge to be detected, spiders had to move at least > 0–3 m. The Adjacent Grid mark-recapture was done after the entire mark-recapture study for Dispersed Grid was completed. Dispersed Grid detected no long distance movement of spiders around the ponds, so we decided to arrange the Adjacent Grid plots in a close adjacent pattern to determine if movement occurred at a smaller scale.

We used Pollock’s (1982) robust mark-recapture sampling design with three primary (long) sampling periods (for Dispersed Grid: 1, 5 and 25 d; for Adjacent Grid: 1, 4 and 8 d), each containing two secondary (short) sampling periods (morning and afternoon of each primary sample date), to estimate movement probability while taking into account variation in detection probability at different sample times. Due to the abundance of spiders in the study area and the difficulty in uniquely marking individuals of such small size (<10 mm in length), we performed our study on spatial cohorts of animals (one per plot), which limited the number of colored marks to

5 per animal. In the morning of day one of sampling for Dispersed Grid we systematically hand-searched each of the nine plots for 20 min, collecting as many wolf spiders as possible. The searches were started on the perimeter of each plot to limit the number of spiders chased out. The intense searches may have caused slight disturbance to the plots, but there was evidence in this system that searching would yield more spiders, especially of sedentary *Pirata* species than passive trapping (Kraus 2006). Spiders from each plot were marked with a different color of non-toxic model paint on their abdomen so we were able to estimate cohort movement rates. The spot was made with the blunt end of a dissecting needle so it would be small enough to not impede their movement or increase predation on the spider. We have some evidence that we were fairly successful achieving these objectives although survival rates increased by about 10% after the first primary period, indicating some mortality may have been caused by the marking process (see Results). The spiders were released around noon. That afternoon the plots were searched again, for 20 min in each plot. These spiders were recorded, marked a different color and released. We repeated the procedure on day five and day twenty-five. Each spider received a maximum of five spots, with each sampling period and plot having a different color. For Adjacent Grid, we used the same Pollock’s Robust design but LA searched alone for 10 min instead of 20 min in each plot, because of the smaller size of the plots and the relatively good capture probability (12–74%).

Data analyses.—Mark-recapture data were analyzed using Program MARK (Version 4.0, downloaded July 2004; White & Burnham 1999). Due to small sample movement rates among plots, which disallowed individual estimates of movements between each plot, each grid was condensed laterally such that vertical (away from and towards the ponds) movement rates of spiders could be estimated and condensed vertically such that lateral (around the perimeter of the ponds) movement rates of spiders could be estimated. We used the Multistrata recapture setting in MARK, because on a few occasions there was movement within a primary period, which violates an assumption of Pollock’s Robust design. All analyses are therefore performed within the

Multistrata framework; the language used to describe sampling intervals in the results section reflects this switch. Survival (s) is the probability of survival from one recapture event to the next, capture probability (p) is the probability of capturing an individual given that the individual is in the plot, and transition probability (ψ) is the probability of moving from one sample plot to the next. The variable “ t ” refers to the time between recapture events in days and “ d ” refers to the linear distance in meters between sample plots.

Our most fully specified model, $p(\cdot)s(\cdot)$, made the simplifying assumption that survival and recapture probabilities would be constant across short sampling intervals and across long sampling intervals within each grid type (dispersed vs. adjacent, see above). We predicted that these assumptions would be valid if movements were small and if survival was similar over the month of sampling. We did not expect movements of all species to be small based on another movement study (Kiss & Samu 2000). However, data on desiccation rates did suggest that *Pirata* species might be constrained to living near the pond edge (Devito et al. 2004), which could limit movement. It seemed probable that survival would be similar over the study since the number of reproductive adults at this site is still increasing at this point in the season (J.M. Kraus, unpublished data).

Based on the fully specified model, we developed four additional models, which constrained movement probabilities in different ways. We varied the parameters in this way to determine the role time and distance played in modeling spider movement. We predicted that distance and time would play a role, but only if movement was limited. First, we constrained movement to be constant by both time and distance, $p(\cdot)s(\cdot)\psi(\cdot)$, essentially saying that the distance between plots did not make a difference to the probability that a spider would move that distance and that the length of time a spider had to move did not affect the probability it would move.

The second model constrained movement to be constant by distance but not time, $p(\cdot)s(\cdot)\psi(\cdot, t)$. The probability of movement between the longer distances was constrained to be the same as the probability of movement between shorter distances. The probability of movement, however, was different for shorter

periods of time (3 h) than longer periods of time (5 or 25 d). In the third model movement was constrained to be constant by time, but not distance, $p(\cdot)s(\cdot)\psi(d, \cdot)$. The length of time a spider had to move did not affect the probability it would move. The distance a spider had to move did affect the probability that it would move that distance. In the fourth model movement was not constrained by time or distance: the probability of moving was allowed to be different for long versus short distances and long versus short sampling intervals, $p(\cdot)s(\cdot)\psi(d, t)$.

We tested the assumption that capture probabilities were constant between sampling periods (i.e., not time variable) with a final model that constrained movement and survival, but not capture probability, $p(t)s(\cdot)\psi(\cdot)$. These models were each applied to the four sets of condensed data (Dispersed Grid vertically condensed, Dispersed Grid laterally condensed, Adjacent Grid vertically condensed, and Adjacent Grid laterally condensed), and then we used Akaike's Information Criterion corrected for small sample size (AIC_c, Akaike 1985) to choose the best-fit model.

RESULTS

A total of 499 spiders with 105 different capture histories were found and marked in Dispersed Grid. Of these, 80% were *P. cantralli*, 10% were *P. sedentarius*, 7% were *P. milvina* and the remainders were *P. montanus* and *P. moesta*. Forty-three percent of wolf spiders marked were juveniles, 28% were females, 17% were males, and 12% were females with egg sacs. Adjacent Grid yielded 147 spiders with 74 capture histories. The majority of spiders in Adjacent Grid were *P. cantralli* (83.7%). The remaining spiders were 6.8% *P. montanus*, 5.4% *P. milvina*, 3.4% *P. moesta*, and 0.7% *P. sedentarius*. Adjacent Grid had mainly female and juvenile spiders; 31.3% were juveniles, 25.9% were females with egg sacs and 36.7% were female spiders. The remaining 6.1% were males. The number of captures per species, sex within species, and developmental stage was not great enough to separately analyze the movement of each group. All species were analyzed together with the understanding that results are presented for the wolf spider assemblage as a whole but mainly reflect the movement of *P. cantralli*. When the data were condensed lat-

Table 1.—Mean (\pm s.e.) survival (s), capture (p) and movement probabilities (ψ) over entire sampling for Dispersed Grid examining movement to and from the ponds (condensed laterally) with a sample size of 499 spiders. Sampling interval is the time between release of spiders and searching the plots again. The AIC_C score is 980.61, the next best model has an AIC_C score of 983.35.

	Short sample intervals (3 h)	Long sample intervals (5 d and 25 d)
s	0.69 \pm 0.08	0.95 \pm 0.01
p	0.36 \pm 0.05	0.24 \pm 0.04
ψ (adjacent plots)	0.05 \pm 0.02	0.06 \pm 0.03
ψ (non-adjacent plots)	0.00 \pm 0.00	0.05 \pm 0.03

erally for Dispersed Grid the number of different capture histories observed decreased to 70 and when condensed vertically it decreased to 62. The laterally condensed data for Adjacent Grid had 62 different capture histories and the vertically condensed data had 43. All probabilities are presented as daily estimates.

The four data sets had different best-fit models. For Dispersed Grid examining movement around the pond (condensed vertically), the best model was $p(\cdot)s(\cdot)\Psi(\cdot)$. For this model the probability of moving between columns (at least 8–28 m) was 0, while average survival probabilities were high (survival probability across shorter sampling intervals $p \pm$ s.e. = 0.77 \pm 0.09 and survival probability across longer sampling intervals = 0.93 \pm 0.01) The capture probability was unconstrained in this model and ranged from 12–72% for all sample period-plot combinations. Sampling Interval 4 (25 d) had a slightly higher capture probability, although the highest single capture probability was in Interval 1 (3 h); Interval 5 (3 h) also has a high capture probability. There does not seem to be any pattern in the capture probability rates. For Dispersed Grid examining movement to and from the pond (condensed laterally), the best fit model was $p(t)s(\cdot)\psi(d, t)$, which allowed movement across short sampling intervals to be different from movement across long sampling intervals and also let movement between adjacent rows be different from movement between nonadjacent rows. The probability of moving between rows (in this case $> 0-3$ m) was small ($p < 0.06$) for all four possibilities (Table 1).

Table 2.—Mean (\pm s.e.) probability of movement (ψ) for Adjacent Grid examining movement around the ponds (condensed vertically) with a sample size of 147 spiders. Sampling interval is the time between release of spiders and searching the plots again. The AIC_C score is 492.54, the next best model had a score of 498.28.

Sampling interval	Adjacent plots	Non-adjacent plots
1 (3 h)	0.03 \pm 0.03	0
2 (4 d)	0.13 \pm 0.12	0
3 (3 h)	0	0
4 (4 d)	0.22 \pm 0.10	0
5 (3 h)	0.13 \pm 0.10	0

The best-fit model for Adjacent Grid examining movement around the pond (vertically condensed) was $p(\cdot)s(\cdot)\psi(\cdot)$. This model constrained capture probabilities and survival to be constant across short and long sampling intervals. The survival was high across short sampling intervals ($s \pm$ s.e. = 0.77 \pm 0.10) and across long sampling intervals ($s \pm$ s.e. = 0.88 \pm 0.04). The higher survival across the longer sampling period might reflect increased mortality due to the marking procedure in the short term. The capture probability p (\pm s.e.) across short sampling intervals was 0.50 (\pm 0.07) and across long sampling intervals was 0.34 \pm 0.07. The probability of horizontal movement for Adjacent Grid was higher than all estimates of movement in the Dispersed Grid and estimates of vertical movement in the Adjacent Grid (Table 2). For Adjacent Grid examining movement to and from the pond (condensed laterally), two models were equally well fit, $p(\cdot)s(\cdot)\psi(\cdot)$ and $p(\cdot)s(\cdot)\psi(d, \cdot)$, with AIC_C values only 0.04 apart. For both models survival, capture probability, and movement were constrained to be constant across short sampling intervals and constant across long sampling intervals. However, the probability of movement between adjacent rows ($> 0-2$ m) was allowed to be different from the probability of movement between nonadjacent rows ($> 1-3$ m) for one but not the other model. For both models the survival was high and the same; the capture probability (p) was the same for both as well, and the probability of movement ($> 0-3$ m) was between 0.01 and 0.04 (Table 3).

Table 3.—Survival, capture probability and probability of wolf spider movement for Adjacent Grid examining movement to and from the pond (condensed laterally) with a sample size of 147 spiders according to two equally fitting models. Sampling interval is the time between release of spiders and searching the plots again. Means \pm s.e. are given. The AICC score for the first model is 459.35, the second model's AICC score is 459.39, the third best fit model is 461.28.

	Short sample intervals (3 h)	Long sample intervals (4 d)
Model: $p(\cdot)s(\cdot)\psi(\cdot)$		
Survival	0.77 \pm 0.10	0.88 \pm 0.04
Capture probability	0.50 \pm 0.07	0.34 \pm 0.07
Probability of movement	0.02 \pm 0.01	0.02 \pm 0.01
Model: $p(\cdot)s(\cdot)\psi(d, \cdot)$		
Survival	0.77 \pm 0.10	0.88 \pm 0.04
Capture probability	0.50 \pm 0.07	0.34 \pm 0.07
Probability of movement between adjacent plots	0.04 \pm 0.02	0.04 \pm 0.02
Probability of movement between nonadjacent plots	0.01 \pm 0.01	0.01 \pm 0.01

DISCUSSION

In this study, we made two independent estimates of wolf spider movement near Sylvatica Pond. The first, taken from Dispersed Grid, estimated movement 0–3 m to and from the pond and 8–28 m around the pond edge 3 h, 5 d, and 25 d after marking. The second, taken from Adjacent Grid, estimated movement 0–3 m to and from the pond and 0–3 m around the pond edge at 3 h and 4 d after marking. The first estimate suggests spiders had a 0% chance of moving 8–28 m around the pond at all of the time scales used (< 25 d). On the other hand, spiders had a 5–6% chance of moving 1–2 m to and from the pond over 5 or 25 d (but 0% chance of doing so in 3 h). The second estimate suggests that spiders had a 4% chance of moving between adjacent rows (0–2 m) to and from the pond over 3 h or 4 d, but no chance of moving among non-adjacent rows (> 1–3 m). Chances of moving between columns around the pond (0–2 m), however, averaged 5% over 3 h, and 18% over 4 d (calculated from Table 2). Although we detected a relatively small amount of movement in our spiders, infrequent longer-distance movements are probably underestimated (Samu et al. 2003).

We predicted that lateral movement around the pond would be much greater for these spiders than movement to and from the pond due to moisture constraints (DeVito and Formanowicz 2003; Graham et al. 2003). We discovered that movement around the pond was more probable than movement to or from the

pond (up to 18% vs. 4%), but that movements of over 3 m were rare enough to be undetected within the study. Higher movement around than to and from the pond fits what is known about the high desiccation rates of wolf spiders that specialize in habitats near water (e.g., *P. sedentarius*, DeVito et al. 2004), and the importance of aquatic prey to spiders living near freshwater (Kato et al. 2003; Power et al. 2004). However, even taking these limitations into account, the probability of moving distances as short as 0–2 m around the pond edge was relatively small compared to previous estimates of wolf spider movement (Morse 1997; Kiss & Samu 2000). For example, Kiss & Samu (2000) found that marked wolf spiders had completely exited a 900 m² quadrant over several days of trapping near Hungarian alfalfa fields. Morse (1997) also found that intertidal wolf spiders (*Pardosa lapidicina* Emerton 1885) migrating with the tide could move the width of the beach (up to 25 m) in one tidal cycle. However, those spiders that remained in the supratidal on the high beach moved infrequently, employing a sit-and-wait hunting strategy. Cages that were located around our study pond from another study likely impeded the long distance movement of the spiders. However, anecdotal evidence (see below) suggests this impediment most likely only affected *P. milvina*, and not the majority of marked spiders in this study (*P. cantralli*).

Wolf spiders are generally thought of as active hunters. Most do not construct webs to catch prey. Our data show that the spiders in

this study, the majority of which was represented by the water specialist *P. cantralli*, apparently hunt in a small (<1 m) region. However, there was some anecdotal evidence that another common species at the pond is capable of larger scale movement. On one occasion, a marked *P. milvina* was found to have moved at least 7 m around the pond perimeter over a five week time period. *Pardosa milvina*, which is found in early successional habitats and is a good colonizer (Marshall et al. 2000), appears to move more than *P. cantralli* and may be able to track resources over a larger spatial scale around the pond.

Several abiotic and biotic factors including moisture and prey distribution can influence the ability or propensity of wolf spiders to move (Nørgaard 1951; Humphreys 1975). Desiccation tolerance and moisture levels limit the distribution of wolf spiders around ponds (DeVito & Formanowicz 2003; Graham et al. 2003). Furthermore, Kreiter & Wise (2001) found that adult female fishing spiders that have been fed move less frequently than those who have not received a meal. Perhaps those spiders living near the pond edge receive sufficient prey from aquatic sources and therefore may not need to roam. There are differences in the soil moisture and prey abundance in areas around the pond (Kraus 2006; L. Ahrens & J.M. Kraus, unpublished). Such differences may dictate where the spiders are able to hunt for food as well as their abundance within those limits. While probability of movement was not analyzed specifically for the differences in life cycle due to small sample size, further study on these differences could provide useful information about which spiders are most responsible for movement. Movement of wolf spiders is most likely affected, therefore, by a combination of biotic and abiotic factors that pose constraints on the distribution and abundance of wolf spiders at the pond edge.

The spatial scale chosen for this study may have had a large impact on the findings from the model. A scale too large or too small can cause important movement and community interactions to be missed (Kareiva 1990). Our study on wolf spiders was conducted to determine movement at the scale of meters during the summer months, fitting the size of the ponds and the active period of the spiders. A study done over a longer time period or a

smaller scale may reveal seasonal or more local movement patterns.

ACKNOWLEDGEMENTS

We thank H. Wilbur for his mentorship on the project, J. Nichols for statistical help, J. Miller for species identification. M. Swift, F. Samu, V. W. Framenau, and P. Ludwig for editorial comments on the manuscript. We acknowledge the NSF Research Experience for Undergraduates granted to Mountain Lake Biological Station for LA, a Mountain Lake Biological Station Summer Fellowship and a NSF Graduate Research Fellowship granted to JMK for funding this project.

LITERATURE CITED

- Akaike, H. 1985. Prediction and entropy. Pp. 1–24. *In* A Celebration of Statistics: the ISI Centenary Volume, (A.C. Atkinson & S.E. Fienberg, eds.). Springer-Verlag, New York.
- Buddle, C.M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. *Journal of Arachnology* 28:319–328.
- Cain, M.L. 1985. Random search by herbivorous insects: a simulation model. *Ecology* 66:876–888.
- DeVito, J. & D.R. Formanowicz. 2003. The effects of size, sex and reproductive condition on thermal and desiccation stress in a riparian spider (*Pirata sedentarius*, Araneae, Lycosidae). *Journal of Arachnology* 31:278–284.
- DeVito, J., J.M. Meil, M.M. Gerson & D.R. Formanowicz, Jr. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat distributions. *Canadian Journal of Zoology* 82:1119–1125.
- Foelix, R.E. 1996. *Biology of Spiders*. Second edition. Oxford University Press, New York. 330 pp.
- Framenau, V.W. 2005. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae). *Journal of Arachnology* 33:334–346.
- Framenau, V.W. & Elgar, M.A. 2005. Cohort dependent life-history traits in a wolf spider (Araneae: Lycosidae) with a bimodal life cycle. *Journal of Zoology, London* 265:179–188.
- Graham, A.K., C.M. Buddle & J.R. Spence. 2003. Habitat affinities of spiders living near a freshwater pond. *Journal of Arachnology* 31:78–89.
- Hanski, I. 1998. *Metapopulation Ecology*. Oxford University Press, New York. 324 pp.
- Henschel, J.R. 2002. Long-distance wandering and mating by the dancing white lady spider (*Leucorchestris arenicola*) (Araneae, Sparassidae)

- across Namib dunes. *Journal of Arachnology* 30: 321–330.
- Henschel, J.R., D. Mahsberg & H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429–438.
- Hering, D. & H. Plachter. 1997. Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. *Oecologia* 111:261–270.
- Humphreys, W.F. 1975. The influence of burrowing and thermoregulatory behaviour on the water relations of *Geolycosa godeffroyi* (Araneae, Lycosidae), an Australian wolf spider. *Oecologia* 21: 291–311.
- Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* 46:195–212.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London: Biological Sciences* 330:175–190.
- Kato, C., T. Iwata, S. Nakano & D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos* 103: 113–120.
- Kiss, B. & F. Samu. 2000. Evaluation of population densities of the common wolf spider *Pardosa agrestis* (Araneae: Lycosidae) in Hungarian alfalfa fields using mark recapture. *European Journal of Entomology* 97:191–195.
- Kraus, J.M. 2006. Reciprocal subsidies to arthropod food webs at a pond-forest boundary. Ph.D. Dissertation. University of Virginia, Charlottesville, Virginia.
- Kraus, J.M. & D.H. Morse. 2005. Seasonal habitat shift in an intertidal wolf spider: proximal cues associated with migration and substrate preference. *Journal of Arachnology* 33:110–123.
- Kreiter, N. & D.H. Wise. 1996. Age-related changes in movement patterns in the fishing spider, *Dolomedes triton* (Araneae, Pisauridae). *Journal of Arachnology* 24:24–33.
- Kreiter, N. & D.H. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia* 127: 417–424.
- Marshall, S.D., S.E. Walker & A.L. Rypstra. 2000. A test of a differential colonization and competitive ability in two generalist predators. *Ecology* 81:3341–3349.
- Morse, D.H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). *Journal of Arachnology* 25:1–10.
- Morse, D.H. 2000. The role of experience in determining patch use by adult crab spiders. *Behaviour* 137:265–278.
- Moulder, B.C. & D.E. Reichle. 1972. Significance of spider predation in the energy dynamics of forest-floor arthropod communities. *Ecological Monographs* 42:473–498.
- Murakami, M. & S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through bird predation. *Ecology Letters* 5:333–337.
- Nichols, J.D. 1992. Capture-recapture models. *BioScience* 42:94–102.
- Nørgaard, E. 1951. On the ecology of two Lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. *Oikos* 3:1–21.
- Pearce, J.L., L.A. Venier, G. Eccles, J. Pedlar & D. McKenney. 2004. Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiversity and Conservation* 13:1305–1334.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757–760.
- Power, M.E., W.E. Rainey, M.S. Parker, J.L. Sabo, A. Smyth, S. Khandwala, J.C. Finlay, F.C. McNeely, K. Marsee & C. Anderson. 2004. River-to-watershed subsidies in an old-growth conifer forest. Pp. 217–240. *In* Food Webs at the Landscape Level (G.A. Polis, M.E. Power & G.R. Huxel, eds.). The University of Chicago Press, Chicago, Illinois.
- Ramos, M., D.J. Irschick & T.E. Christenson. 2004. Overcoming an evolutionary conflict: removal of a reproductive organ greatly increases locomotor performance. *Proceedings of the National Academy of Science USA* 101:4883–4887.
- Sabo, J.L. & M.E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83:3023–3036.
- Samu, F., A. Sziranyi & B. Kiss. 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. *Animal Behaviour* 66:939–947.
- Uetz, G.W. & J.D. Unzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology* 3:101–111.
- Weins, J.A. 2001. The landscape context of dispersal. Pp. 96–109. *In* Dispersal (J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols, eds.). Oxford University Press, New York.
- White, G.C. & K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement: 120–138.